

UNIVERSITÉ DU QUÉBEC À RIMOUSKI

INFLUENCE DE FACTEURS BIOTIQUES ET ABIOTIQUES SUR LA FORCE
D'ATTACHEMENT DU BYSSUS DE LA MOULE BLEUE (*MYTILUS EDULIS*) EN
CULTURE EN SUSPENSION AUX ÎLES DE LA MADELEINE
(QUÉBEC, CANADA).

MÉMOIRE

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RÉSUMÉ

Les moules possèdent la capacité à s'attacher à leur substrat en produisant des filaments de byssus. Cette caractéristique simplifie grandement le système de culture sur filière immergée dans les provinces Atlantiques du Canada. Par contre, aux Îles de la Madeleine (Golfe du St-Laurent), des pertes par dégrappage (moules tombant en se détachant du boudin) ont été observées durant la période d'été. Ces pertes de moules par dégrappage peuvent être reliées à une diminution de la force d'attachement du byssus des moules par rapport à leur substrat. La présente étude a pour but de déterminer, de façon hebdomadaire, la variation temporelle de la force d'attachement des moules (*Mytilus edulis*) de culture âgées de 2 ans, dans la lagune du Havre-aux-Maisons, (Îles de la Madeleine) de la fin Mai à la mi-Octobre, en relation avec la reproduction et les facteurs environnementaux. Les facteurs environnementaux (température, disponibilité de nourriture, vitesse du vent et conditions hydrodynamiques: vitesse du courant, turbulence de l'eau, hauteur des vagues) et la condition de reproduction ont été mesurés simultanément. La force d'attachement des moules a été mesurée directement sur les boudins à l'aide d'un dynamomètre. La force d'attachement des moules variaient grandement durant la période d'échantillonnage avec des valeurs deux fois plus élevées en automne qu'en été. Cette différence temporelle n'est pas reliée seulement à la variation du nombre de filaments de byssus, mais aussi à leur force individuelle. L'influence de chaque facteur est discutée en relation avec une hiérarchie basée sur leur corrélation avec la force d'attachement. Les résultats suggèrent que la ponte des moules semble être synchronisée avec une diminution importante de la force d'attachement (-32%) à l'intérieur d'une semaine à la fin du mois de juin. Par contre, la température et la turbulence de l'eau sont les facteurs ayant la plus grande influence sur la force d'attachement des moules.

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INTRODUCTION GÉNÉRALE

Mytiliculture

La culture de moules ou mytiliculture s'effectue dans plusieurs régions du monde et plus particulièrement en Amérique du Nord et en Europe, pour l'espèce *Mytilus edulis*, puisque l'aire de distribution de cette espèce est circumpolaire et qu'on la retrouve dans les océans Pacifique nord, Atlantique nord et Arctique (AAFC 2007; FAO 2007). La production mondiale de moules a augmenté de 29 % entre 1991 et 2002. La mytiliculture est implantée au Canada depuis la fin des années 1970 (Mallet et Myrand 1995). En 2005, la production canadienne (22 000 T) représentait seulement une petite partie, soit 1,5 % de la production mondiale (1 444 734 T) (FAO 2007). La mytiliculture prend place surtout dans les provinces de l'Atlantique et y est en majeure partie dominée (81 %) par l'Île-du-Prince-Edouard (MPO 2007). Bien que la production québécoise soit relativement faible, représentant seulement 1,6 % de la production annuelle canadienne avec 753 T, celle-ci a atteint son plus haut niveau en 2005 (MAPAQ 2007). La moule bleue est par ailleurs le plus important mollusque cultivé dans la région du Golfe du St-Laurent (MPO 2007).

Plusieurs techniques sont utilisées pour la production de moules. Les moules peuvent être cultivées sur le fond, comme par exemple aux Pays-Bas et dans le Nord-est américain ou encore sur bouchot, pieux plantés en zone intertidale sur lesquels les moules s'accrochent, technique préconisée particulièrement en France (Mallet et Myrand 1995).

Les moules peuvent également être cultivées sur des cordes en suspension dans la colonne d'eau selon différentes techniques telles que suspendues à des radeaux (Espagne) ou encore à des lignes flottantes immergées comme c'est le cas par exemple au Canada, en Nouvelle-Zélande et en Irlande (Hickman 1992). Ce système inspiré des lignes flottantes utilisées pour la culture de pétoncles et d'huîtres au Japon est très bien adapté au couvert de glace hivernal que l'on retrouve dans le Canada Atlantique (Hickman 1992, Mallet et Myrand 1995). Au Québec, le système de culture est constitué d'une ligne (filière) principale horizontale et immergée sur laquelle sont attachés les boudins de moules, le tout étant retenu au fond par des ancrages et maintenu dans la colonne d'eau par des bouées de flottaison (Figure 1). La technique principalement utilisée au Québec est le boudinage mécanisé en continu qui a été largement inspiré de l'approche utilisée en Nouvelle-Zélande, mais modifiée avec des éléments provenant de l'approche espagnole. Le cycle de production de la moule bleue débute par une période de captage des larves qui se fixent sur des collecteurs artificiels, comme des cordes suspendues dans la colonne d'eau. Les jeunes moules sont ensuite détachées des collecteurs, triées mécaniquement selon leur longueur et boudinées (placées) dans un filet tubulaire de coton biodégradable entouré d'une ficelle de lin. Une corde de polypropylène est placée au centre de cet ensemble, et c'est sur cette structure plus solide que les moules vont s'attacher, avant que le filet et la ficelle ne se dégradent. Ceci va former un long boudin qui sera par la suite accroché à intervalles réguliers à la filière flottante immergée (CSMOPM 2007). La densité des moules dans les boudins est un facteur important à contrôler afin d'éviter des pertes trop importantes dues au poids excessif de ces moules sur les boudins, ainsi qu'une compétition intraspécifique

réduisant la croissance des moules (Mallet et Carver 1991). Les moules vont croître sur le boudin jusqu'à l'atteinte de la taille commerciale de 50 mm, qui nécessite entre un à trois ans selon le site et la croissance des moules, puis elles seront récoltées et mises en marché (Mallet et Myrand 1995). Bien que l'on retrouve deux espèces de moules bleues dans l'Atlantique nord soit *Mytilus trossulus* et *Mytilus edulis* (Gosling 1992), cette dernière représente plus de 95% de la population de moules cultivées aux Îles de la Madeleine (Myrand *et al.* 2002). C'est pourquoi il est possible dans la présente étude de ne faire référence qu'à l'espèce *M. edulis*.

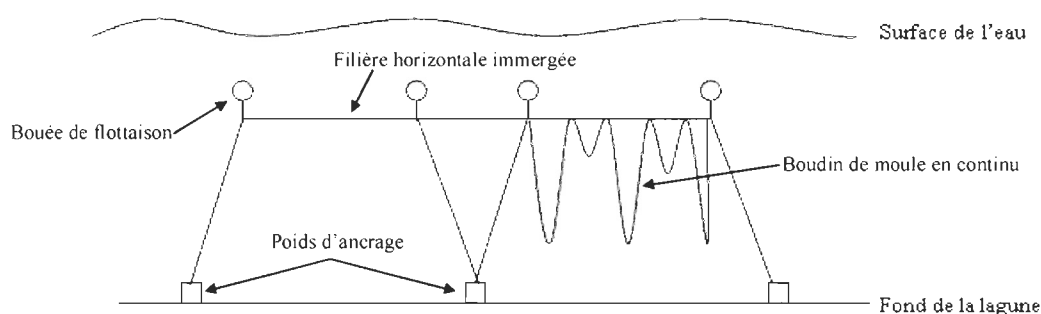


Figure 1. Schéma de la production de moule en boudins continus suspendus dans la colonne d'eau. Schéma modifié à partir de celui de Leonard (2004)

Pertes de moules (chute sur le fond à partir des boudins)

Durant la dernière étape de la production qu'est la croissance sur boudins, des pertes de moules peuvent occasionner une diminution importante de la production et donc de

revenus pour les producteurs. Les pertes de moules peuvent être de différentes natures. D'abord, il y a une perte normale de moules au cours de la production due à l'ajustement continu de la densité en fonction de la taille des moules qui prennent plus d'espace en croissant. Il est possible de limiter ces pertes en évitant les densités excessives de moules au moment du boudinage (Fréchette *et al.* 1996). À cela s'ajoute les pertes par la prédation causées majoritairement par le crabe commun (*Cancer irroratus*) et par l'étoile de mer *Asterias sp.* (Mallet et Myrand 1995, Bourque et Myrand 2006). Les pertes par prédation peuvent être diminuées en bonne partie par de bonnes pratiques mytilicoles comme, par exemple, en évitant que les boudins touchent au fond grâce à une gestion appropriée de la flottabilité des lignes flottantes. Une autre source de pertes importantes de moules est la mortalité massive estivale qui a déjà touché durement la production mytilicole des Îles de la Madeleine (Myrand et Gaudreault 1995). Cette mortalité massive serait causée par l'effet synergique d'un métabolisme de base élevé, de la baisse d'énergie résultant de la ponte des moules simultanément à des conditions stressantes associées à une température élevée de l'eau dans les lagunes (Tremblay *et al.* 1998a). Ce problème a été en grande partie réglé avec l'utilisation d'un stock génétiquement différent (celui de Havre-Aubert) offrant une meilleure résistance au stress (Myrand *et al.* 2000). Bien que la mortalité de moules puisse être une source importante de la diminution de biomasse, des pertes par dégrappage peuvent également occasionner d'importantes réductions des rendements commerciaux (Mallet et Carver 1991, Mallet et Myrand 1995, Inglis et Gust 2003). Ces pertes par dégrappage sont de deux niveaux: dégrappage passif pendant le cycle de production et dégrappage à la récolte lorsque les boudins sont sortis de l'eau et hissés à bord des

embarcations. Les pertes par dégrappage au moment de la récolte peuvent être importantes, mais une conception adéquate des équipements de récolte permet d'en limiter l'ampleur (Bourque et Myrand 2006). Les pertes par dégrappage passif sont par ailleurs observées régulièrement durant l'été dans les lagunes des Îles de la Madeleine. De plus, ces pertes s'avèrent plus importantes sur les boudins de moules de deux ans que sur ceux d'un an (Leonard 2004). Par conséquent, l'impact sur la rentabilité est encore plus important puisque ces moules sont en fin de cycle de production. Par exemple, on a déjà observé des pertes pouvant atteindre 7,2 kg de moules par mètre de boudins de 2 ans entre la fin juin et le début septembre (B. Myrand, données non publiées). Ce problème de pertes par dégrappage est exclusif à la culture de la moule. En effet, la mytiliculture utilise la capacité de la moule à s'accrocher elle-même à un substrat par ses filaments de byssus contrairement à d'autres cultures de bivalves, telle que celle du pétoncle (MAPAQ 2007). Peu importe le type de dégrappage, les pertes pourraient être associées, en bonne partie, à une diminution de la force d'attachement des moules sur les boudins (Mallet et Carver 1991, Mallet et Myrand 1995). Moins solidement attachées, les moules deviennent alors plus vulnérables aux facteurs entraînant les chutes (poids excessif, turbulence, travail sur les lignes d'élevage, sortie de l'eau,...).

Le byssus

L'attachement des moules au substrat se fait par l'entremise du byssus. Celui-ci est composé de plusieurs filaments, sécrétés par la glande byssale localisée dans le pied de la

moule. Ce sont ces filaments qui se collent au substrat, permettant ainsi à la moule de s'ancrer solidement (Figure 2) (Mahéo 1970, Waite 1983, Carrington 2002a).

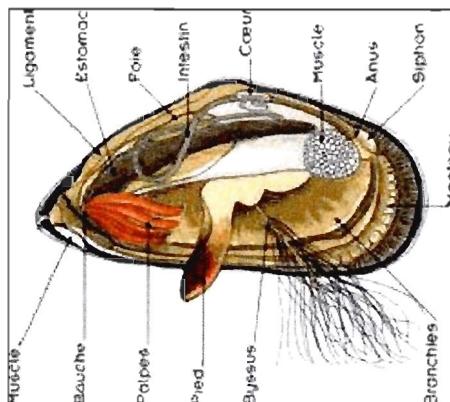


Figure 2. Schéma de l'anatomie de la moule montrant le pied et le byssus. Tiré du comité national de la conchyliculture 2007

Le processus de sécrétion du byssus débute tout d'abord par la sortie du pied de la moule hors de la coquille. Celui-ci explore alors le milieu au contact du substrat pour assurer un solide point d'ancrage à la moule. L'extrémité du pied s'aplatit contre la roche, ou autre matériau solide, puis s'immobilise durant une à deux minutes. À ce moment, la glande byssale déverse une substance blanche dans le canal ventral du pied relié à la dépression distale située à son extrémité (Figure 3). La substance blanche accumulée dans la dépression distale se fixe au substrat et forme ce que l'on appelle la plaque. La substance blanche durcit à l'intérieur du canal et forme un filament de byssus avec ses parties distale et proximale, la dernière étant reliée à la colonne d'où partiront tous les filaments nouvellement formés. Cette colonne est elle-même reliée à la racine enfoncée dans la

région basale du pied et reliée au muscle rétracteur (Figure 3). Le pied se relâche enfin pour libérer le filament de byssus. La moule dispose ses filaments de byssus de façon radiale (Smeathers et Vincent 1979, Price 1983, Bell et Gosline 1997). Elle secrète en moins de 24 heures les filaments nécessaires à son attachement, tandis que la sécrétion ultérieure de filaments est plus lente et dépend essentiellement des conditions du milieu (Mahéo 1970). Après la période de 24 heures, environ 95% des filaments sécrétés lors de cette période sont encore en bon état, pour une moule de 60 mm de longueur (Allen *et al.* 1976). Les filaments se dégradent et doivent continuellement être remplacés par de nouveaux (Mahéo 1970, Lee *et al.* 1990). Selon Price (1981), la force et la rigidité des filaments de byssus diminuent significativement après une période de 25 jours et la durée de vie d'un filament de byssus serait de 4-6 semaines (Carrington 2002b). Peu d'études ont été effectuées sur la vitesse de dégradation des filaments de byssus. Une étude récente démontre que la dégradation de ces filaments varie en fonction de la saison (Moeser et Carrington 2006). Le nombre de filaments qui fixent la moule au substrat se situe habituellement entre 20 et 60 (Bell et Gosline 1996). La production de byssus représente environ 8% de la dépense énergétique totale d'une moule adulte (Griffith et King 1979, Hawkins et Bayne 1985).

De plus, la moule possède la capacité à se détacher de son substrat lorsque les conditions du milieu ne lui sont pas favorables ni optimales (Mahéo 1970, Price 1983, Lee *et al.* 1990, Hunt et Sheibling 2002). La moule se détache de son byssus par l'entremise de sa musculature interne, elle rompt donc son byssus par traction et se déplace en rampant sur le substrat à l'aide de son pied (Mahéo 1970). La moule peut également être détachée

involontairement par les vagues et dans ce cas comme dans le précédent elle doit par la suite se rattacher à un nouvel endroit, reconstituant son byssus rapidement pour éviter de se faire déloger (Mahéo 1970, Hunt et Sheibling 2002).

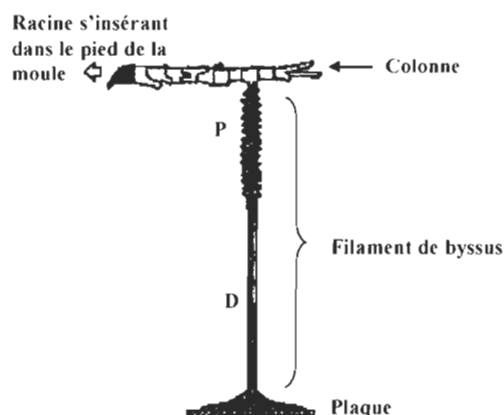


Figure 3. Schéma présentant les différentes parties composantes du byssus de moule. P (partie proximale) et D (partie distale) du filament de byssus. Schéma modifié à partir de celui de Van Hest et Tirrell (2001)

Les filaments de byssus sont composés principalement de plusieurs protéines différentes, la plus abondante étant le collagène (Price 1983, Waite 1983, Gosline *et al.* 2002). Le collagène confère une très grande résistance aux filaments. De plus, les filaments sont très élastiques, ce qui leur permet une déformation réversible. Ces deux caractéristiques, la résistance et l'élasticité, constituent la clé de l'attachement et donc de la survie des moules dans leur environnement (Bell et Gosline 1996, Gosline *et al.* 2002). La quantité des filaments de byssus produits par la moule peut influencer sa force d'attachement (Price 1980, Bell et Gosline 1997, Pelc et Alexander 1999). La force

d'attachement représente la force nécessaire requise pour maintenir ancrée la moule au substrat. En plus du nombre de filaments produits, les propriétés individuelles (force, épaisseur) des filaments de byssus peuvent aussi influencer la force d'attachement des moules (Bell et Gosline 1997).

La plupart des études portant sur le byssus des moules sauvages se sont intéressées à l'effet de la variation de différents facteurs environnementaux sur la production des filaments de byssus que ce soit en nombre ou en taux de production de filaments. Ces études ont majoritairement été effectuées en laboratoire, dans des conditions contrôlées en isolant l'effet de chacune des variables étudiées. Ces études ont démontré par exemple, que le nombre de filaments augmente avec la température jusqu'à 25°C, tandis qu'il diminue avec une baisse de la salinité ainsi qu'avec une faible disponibilité en nourriture. La production de filaments de byssus semble également augmenter avec les courants, l'agitation de l'eau, la turbidité, et la présence de prédateurs (Young 1985, Lee *et al.* 1990, Carrington Bell et Denny 1994, Dolmer et Svane 1994, Cote 1995, Bell et Gosline 1997, Dolmer 1998, Clarke 1999, Selin et Vekhova 2004, Alfaro 2005). Bien que ces études apportent de précieuses informations quant aux facteurs influençant la production de filaments de byssus, l'utilisation de ces informations en vue d'une meilleure compréhension de ce qui se passe en milieu naturel est difficile, puisque les facteurs du milieu peuvent être confondus au niveau de l'importance de leur influence individuelle respective. Il y a cependant quelques études qui ont été réalisées sur des moules sauvages en milieu intertidal afin de déterminer les facteurs prédominants et d'expliquer la variation de la production de

byssus ou de la force d'attachement. Ces études sont donc plus près de la réalité des moules en milieu naturel puisqu'elles intègrent à la fois des facteurs environnementaux et physiologiques. Ces études en milieu intertidal révèlent une variation temporelle de la force d'attachement couplée à la variation de différents facteurs comme la force des vagues et la condition de reproduction des moules (Price 1980, Price 1982, Hunt et Scheibling 2001, Carrington 2002b). Toutefois, l'échelle temporelle de l'échantillonnage à une fréquence mensuelle peut diminuer la précision des résultats et masquer des relations possibles à plus petite échelle.

De plus l'influence relative de chacun de ces facteurs sur la variation de la force d'attachement pourrait être différente pour les moules d'élevage comparativement aux moules sauvages étant donnée la différence de l'environnement qui les entoure (suspendues dans la colonne d'eau dans un plan d'eau bien abrité vs zone intertidale rocheuse). Jusqu'à présent la force d'attachement a été étudiée sur les moules sauvages vivant dans le milieu intertidal mais jamais sur des moules d'élevage en suspension. D'où l'importance et l'aspect innovateur de la présente étude.

BUT ET OBJECTIFS

Le but de cette étude est d'évaluer la variation temporelle de la force d'attachement des moules de culture (*Mytilus edulis*) aux îles de la Madeleine situées dans le Golfe du St-

Laurent, Canada, et d'identifier les facteurs pouvant l'influencer. Le premier objectif de l'étude est de mesurer la force d'attachement des moules de deux ans directement sur les boudins prélevés dans la lagune du Havre-aux-Maisons. La force d'attachement a été mesurée sur une base hebdomadaire, de la fin mai à la mi-octobre 2005, fournissant ainsi une plus grande précision que les études antérieures où ces mesures n'étaient effectuées qu'à une fréquence mensuelle. Notre hypothèse pour le premier objectif, est que la force d'attachement varie durant la période d'échantillonnage. Le deuxième objectif spécifique vise à déterminer l'influence éventuelle de différents facteurs sur la variabilité de la force d'attachement. Ainsi, l'état reproducteur (facteur physiologique) des moules dont on a mesuré la force d'attachement a été déterminé. Parallèlement aux mesures d'attachement, des données environnementales ont été mesurées et enregistrées pour caractériser les conditions ambiantes au site d'échantillonnage. Ces données comprennent la température de l'eau, la disponibilité de la nourriture, la vitesse du vent et les caractéristiques hydrodynamiques : la hauteur des vagues, la force du courant, la turbulence de l'eau. Dans un deuxième temps, tous ces facteurs explicatifs ont été examinés en fonction de leur lien avec la variation de la force d'attachement. L'hypothèse reliée au deuxième objectif est que la force d'attachement est surtout corrélée à la reproduction des moules et à la turbulence dans l'eau. Le dernier objectif vise à déterminer si la force des filaments individuels de byssus des moules varie dans le même sens que la force d'attachement globale des moules avec comme hypothèse une relation positive entre ces deux mesures de force d'attachement.

**CHAPITRE 1 : BIOTIC AND ABIOTIC INFLUENCES ON THE
ATTACHMENT STRENGTH OF BLUE MUSSEL (*MYTILUS EDULIS*) FROM
SUSPENDED CULTURE, IN THE MAGDALEN ISLANDS (QUEBEC, CANADA).**

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ABSTRACT

Mussels can attach themselves to solid substrata by producing byssal threads. This behavior greatly simplifies their cultivation on submerged longlines. However, fall-off of mussels from sleeves have been observed during summer in the Magdalen Islands, Gulf of St. Lawrence, Canada. Such fall-off can be related to the variation in the attachment strength of the mussels to their culture substrate. This study examined on a weekly basis the temporal variation of attachment strength of 2-year-old cultured mussels (*Mytilus edulis*), from late May to mid-October, in the House Harbour lagoon (Magdalen Islands). This study examined some possible influential factors of attachment strength. Environmental factors (temperature, food availability, wind velocity and hydrodynamic conditions: current velocity, turbulence, waves height) and reproductive condition were measured concurrently. Attachment strength was measured directly on mussels from sleeves with a dynamometer. Attachment strength varied twofold from summer to fall, a difference related not only to the number of byssal threads but also to their individual strength. The influence of each factor is discussed relative to a hierarchy based on their correlation with attachment strength. Our results suggest that spawning seemed to be synchronized with a major decrease (-32%) in attachment strength within one week in late June and that water temperature and turbulence were the most important factors explaining the variation in mussel attachment strength afterwards. In contrast to previous studies, no trade-offs were observed between reproduction and attachment strength.

1.1 INTRODUCTION

Mussel growers take advantage of a characteristic behavior of mussels, namely their capacity of self-attachment to substratum, to get a simplified culture system avoiding containment in cages, trays, etc. In Atlantic Canada, mussels are mostly produced in suspended culture on submersible longlines to provide against the ice cover (Mallet and Carver 1991, Mallet and Myrand 1995). Soon after sleeving, the young mussels attach themselves to the culture substratum (rope) where they will grow up until the harvest time about 12 to 18 mo later (Mallet and Myrand 1995). However, fall-off or slippage of mussels from sleeves may occur during the production cycle and may lead to substantial biomass losses (Grant *et al.* 1995, Mallet and Myrand 1995, Inglis and Gust 2003). Fall-off of mussels from sleeves can represent substantial losses of 742.3 ± 492.3 kg/day in July at the culture sites in the House Harbour lagoon (Leonard 2004). Factors inducing these fall-offs are poorly understood. As mussel attachment strength is variable (Carrington 2002b), fall-offs may be, at least partly, the result of a weaker attachment of the mussel byssus.

The byssus, composed of multiple extracellular collagenous byssal threads secreted by a gland in the foot, tethers the mussel to its substratum. Byssal threads have a limited lifetime (likely 4-6 weeks) and decaying threads must be replenished (Carrington 2002b). Thus the mussel must secrete new threads regularly to stay attached to the substratum. In most of the studies on attachment strength of mussel byssus, the number of threads is used to characterize attachment strength (more threads = stronger attachment) and single

explanatory factors are usually under controlled investigation (Young 1985, Lee *et al.* 1990, Dolmer and Svane 1994, Cote 1995, Dolmer 1998, Clarke 1999, Selin and Vekhova 2004, Alfaro 2005). In other studies, attachment strength is defined as the force a mussel needs to stay attached to its substrate. Such studies have usually been performed in field conditions on wild mussels attached to rocky shores (Price 1982, Carrington 2002b, Zardi *et al.* 2007).

A number of factors can influence the attachment strength of mussels in natural populations. For example, byssal thread production (and thus attachment strength) increased with water temperature ranging from 0 to 25°C, but is inhibited above 26°C (Young 1985, Lee *et al.* 1990, Selin and Vekhova 2004). Food availability can also influence attachment strength by decreasing threads production when food is limited (Price 1980, Young 1985, Clarke 1999, Carrington 2002a). Mussels living in the intertidal zone are also challenged by hydrodynamic forces generated by wave action (Price 1982, Carrington Bell and Denny 1994, Bell and Gosline 1997, Carrington 2002b, Hunt and Sheibling 2002), and byssal thread production depends on various aspects of water motion, such as current velocity (one-directional water motion) (Lee *et al.* 1990, Dolmer and Svane 1994, Bell and Gosline 1997, Alfaro 2005, Moeser *et al.* 2006) and turbulence (multi-directional water motion) (Mahéo 1970, Van Winkle 1970, Young 1985). Current velocity, which is often associated to wave action in intertidal zone, was generally used in studies to characterize the hydrodynamic forces instead of the water turbulence. In addition to exogenous factors like those cited above, endogenous factors like reproductive condition

may also be linked to mussel attachment strength (Hawkins and Bayne 1985, Seed and Suchanek 1992). Several studies observed an inverse relationship between reproductive cycle and attachment strength, suggesting that mussels may not always have available energy for byssal thread production, specifically when gamete production occurred (Price 1980, Price 1982, Carrington 2002b, Zardi *et al.* 2007). Mussel attachment strength does not just depend on the number of byssal threads produced, but also on the material properties of the threads (Moeser and Carrington 2006).

Since so many factors can influence attachment strength of mussels, it is not surprising that mussel attachment strength fluctuates with the seasons in natural populations (Price 1980, Price 1982, Hunt and Scheibling 2001, Carrington 2002b). Many of the factors cited above naturally covaried, making it difficult to determine which factors are most important in determining attachment strength. Several studies of wild mussels living in the intertidal zone suggest an influential role by wave action (Price 1980, Price 1982, Hunt and Scheibling 2001, Carrington 2002b). Cultured mussels, however, are kept on ropes suspended in the water column in sheltered areas where environmental factors such as waves, current velocity and turbulence may not have the same influence on the attachment strength. No studies have ever been done on attachment strength of suspension-cultured mussels.

The main purpose of this study was to examine the temporal variation of attachment strength of suspension-cultured mussels (*Mytilus edulis*) in the Magdalen Islands, Gulf of St. Lawrence, Canada, and to identify explanatory factors. Magdalen Islands lagoons are characterized by the presence of *Mytilus edulis* species at level over 98% (Tremblay *et al.* 1998b). The first specific objective was to measure mussel attachment strength on sleeves from spring to fall on a weekly basis, a more frequent sampling regime than in all previous studies based on monthly samplings. The hypothesis for this objective was that attachment strength varied during the sampling period. Concurrently, mussel reproductive condition was quantified and environmental characteristics were monitored: temperature, food availability, wind velocity and hydrodynamic conditions (current velocity, turbulence, wave height). A hierarchy of the factors was established according to their relationship with attachment strength of mussels. We hypothesized that reproductive condition and water turbulence will be positively correlated to attachment strength and that they will be the most important factors influencing it. A second objective consisted in the evaluation of the material strength of individual byssal threads at two different periods (summer and fall). The hypothesis for this second objective was that the strength of individual threads will vary in the same way than mussel byssus attachment strength.

1.2 MATERIALS AND METHODS

A preliminary study was conducted in 2004 from June 25 to October 13 and this effort guided a more extensive sampling in 2005 (longer sampling season and improved

monitoring of the water column characteristics). Thus the main experiment occurred from May 24 to October 17 in 2005 with attachment strength measurement, reproductive condition determination, seston characterization and environmental monitoring of the water column. The less extensive data of 2004 are presented as a useful comparison.

1.2.1 *Site*

Experiments took place in the House Harbour lagoon in the Magdalen Islands (Quebec, Canada), where blue mussels (*Mytilus edulis*) are cultivated (Figure 4). The maximal depth of the House Harbour lagoon and at the experimental site is approximately 6 m. The lagoon communicates with the open sea by a relatively narrow channel. The maximum tidal amplitude is only about 0.5 m inside the lagoon (Koutitonsky, unpub. data). Tidal currents velocities are relatively low in the basin ($< 0.05 \text{ m s}^{-1}$); wind is very important in mixing of the water column of this shallow lagoon (Koutitonsky *et al.* 2002, Koutitonsky and Tita 2006).

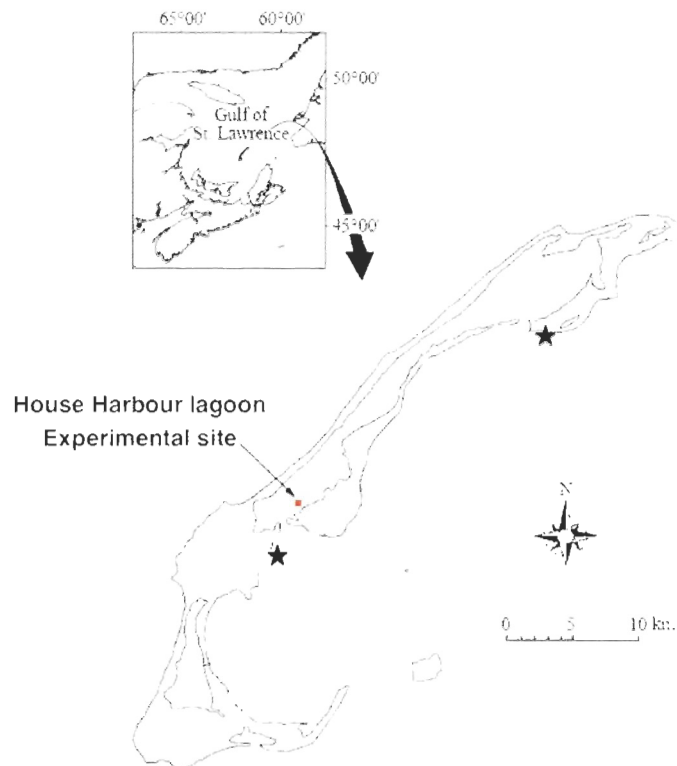


Figure 4. Location of the experimental site in the House Harbour lagoon in the Magdalen Islands. The two dark stars indicate the position of the tidal gauges

1.2.2 Attachment strength and reproductive condition

Sections of 2-year-old commercial mussel sleeves (approximately 60 cm long) were prepared in spring (early May) when mussels are tightly attached to the culture substrate (polypropylene rope) and suspended on a submerged longline kept at about 2 m from the surface, at the experimental site. Two-year-old mussels have been chosen instead of 1-year-old mussels because they have an important reproductive effort and a limited growth avoiding the introduction of the shell length as a possible confounding factor and also

because the fall-off of these mussels is more important in suspension culture (Leonard 2004). Every week three sections of sleeves (thereafter referred to as “sleeves”) were harvested randomly from the longline, brought back carefully to the laboratory and kept vertically in a flow-through tank supplied with seawater pumped from the lagoon until attachment strength was measured (within 24 hours).

Attachment strength was measured weekly on 45 mussels (15 mussels per sleeve) in 2004 and on 30 mussels (10 mussels per sleeve) in 2005. The sleeve was first fixed horizontally and tightly on a wooden board with a net. The mussels chosen for measurement were positioned in the outer surface of the sleeve (not overgrown by neighbors) and oriented with their long axis perpendicular to the sleeve (Figure 5). The net was cut just around the mussel and a small hole was drilled through the mussel shell. A hook was inserted in the hole and connected to a digital dynamometer (AFG 250 N \pm 0.05 Quantrol TM; Dillon, Fairmont, MN, USA) fixed on an endless screw stand just above the mussel. The mussel was pulled vertically from the sleeve with a small motor running at constant low speed until complete dislodgment of this mussel occurred, ascertaining that just one mussel was being pulled up. The maximal force (measured in Newton) applied before dislodgment was recorded using QGraph Quantrol TM software (Dillon, Fairmont, MN, USA) and represented the attachment strength. Only mussels at the outer surface of the sleeves could be measured due to the impossibility of measuring mussels inside of the sleeve without disturbing all the mussels assemblage. This method measured the global rather than the self-attachment strength of a given mussel because the mussels on a sleeve

attach their byssal threads to the shells of their neighbours. As a result, the experimental mussels were kept attached to the sleeve by their neighbours threads as well as by their own byssal threads, while pulled up by the dynamometer. The sleeves were kept wet during the measurement. After attachment strength measurement, shell length was measured using a vernier calliper. As the range of mussel size was small within all the samples (mean length \pm S.D.: 68.3 ± 5.0 mm, $N= 630$) there was no need to normalize the attachment strength to mussel size (E. Carrington, pers. comm.). Each mussel was dissected and the gonad index was calculated as the dry mantle weight (72 hours at 70°C) divided by the whole body weight (the sum of the dry weights of the mantle and remaining tissues).

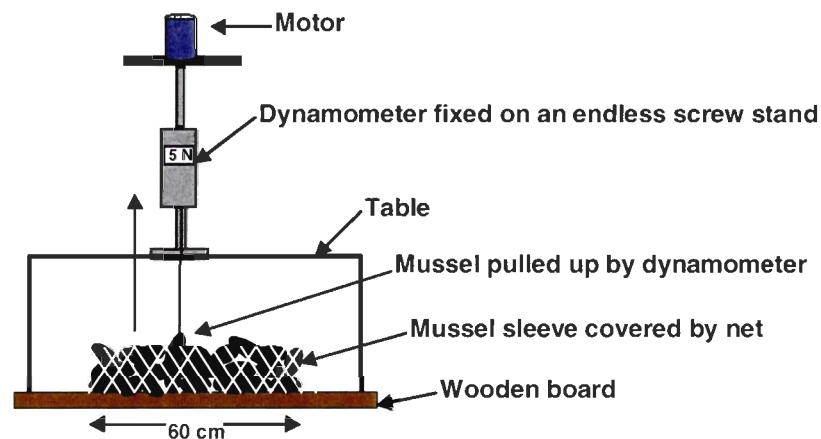


Figure 5. Measurement of attachment strength of cultured mussels on sleeve with a dynamometer. Black circles corresponded to mussels in a 60 cm long sleeve

1.2.3 *Individual force of byssal threads*

An additional 10 mussels were taken haphazardly from sleeves at two different dates in the summer (August 02, 2005) and fall (October 17, 2005) following the attachment strength measurements. Mussel byssus was removed carefully from its substrate, thread by thread, at the plaque region of the thread and the byssus was cut off at the shell margin (corresponding to the proximal region of the thread). Byssus were then dehydrated by air exposure in an open plastic bag until tensile tests were performed (Brazee and Carrington 2006). The byssus (byssal threads and stem) of each mussel was rehydrated 30 minutes in seawater before testing. The two ends of the byssal threads (distal or disc region and proximal or stem region) were mounted within a pair of grips using cardstock and cyanoacrylate glue, which were attached to a mobile crosshead of an Instron 5565 tensometer (Instron, Canton, MA, USA) (Moeser and Carrington 2006). Threads were submerged in seawater at 15°C and extended $10 \text{ mm} \cdot \text{min}^{-1}$ until failure occurred. Force (± 0.02 Newtons) was recorded every second and the maximum value was used as the thread strength.

1.2.4 *Seston characterization*

During each weekly sampling, three 2-l water samples were taken with a Niskin bottle at the mussel sleeves level. The seawater was kept in cool conditions in the dark until filtration for seston characterization within the same day. Then each sample of seawater

was filtered through washed and pre-weighted GFC filters. Filters were dried and weighted following the method of Aminot and Chaussepied (1983) to obtain the total particulate matter (TPM) and the particulate inorganic matter (PIM). The seston component used in this study is the particulate organic matter (POM) and it was calculated by subtracting PIM from TPM.

1.2.5 *Environmental monitoring*

To monitor the water column characteristics, an Acoustic Doppler Current Profiler (ADCP) Workhorse Sentinel 1200 KHz[™] (RD Instruments, Inc. San Diego, CA, USA) and an Acoustic Doppler Velocimeter (ADV) Vektor 6 MHz[™] (Nortek, Annapolis, USA) were placed near the bottom of the House Harbour lagoon next to the experimental longline from June 15 to October 19 2005. The ADCP measured the current velocity at 30 cm depth intervals throughout all the water column every 20 minutes, but only current velocity data recorded at the sleeves level were used in the analysis. The ADV measured the turbulence 50 cm above the bottom surface at 8 hz. The ADV probe components consisted of an acoustic transmitter and 3 acoustic receivers measuring water velocity in the x, y and z axes. The ADV measured water temperature every 60 minutes. It measured also the wave height every 20 minutes using data recorded during a period of 5 minutes at 8 hz. The wind velocity data has been measured by Environment Canada at the local airport about one kilometre away from the experimental site. Two tide gauges Coastal Leasing Micro Tide 2 Hz[™] with a 20-minutes interval recording were placed at two different sites (Figure 4). Tide

and current tide data were used in the calculations of hydrodynamic parameters. For all the water column data, daily mean values were calculated from the hourly values and weekly means were then determined from the daily mean values. Significant wave height (H_s) corresponded to the average height of the highest one-third of all waves occurring in a particular time period (Open University 1989) and was used as the wave parameter in further analysis. The salinity in the lagoon was not measured due to its stability (28-31 ppt) (Myrand 1991).

1.2.6. *Statistical analysis*

Sample size was 45 mussels per week in 2004 but was decreased to 30 mussels in 2005 following a power statistical analysis. The variation coefficient was determined, for each sampling date with $n = 45$ (15 mussels per sleeve), and compared to the same variation coefficient with $n = 30$ (10 mussels per sleeve). The analysis revealed no important changes in the results precision (Statistical Consultation Services, Hélène Crépeau, Mathematical Department, Laval University, pers. comm.).

All statistical analyses were performed using Systat 11 (Systat Software Inc, San Jose, CA, USA) and data were log- or squared root-transformed when needed to satisfy test conditions. A two-way hierarchical ANOVA tested for a difference in attachment strength between sampling dates, in 2004 and 2005, with date and sleeve (nested factor) as factors.

T-tests with a Bonferroni correction were used for planned comparison tests between successive dates. A one-way ANOVA evaluated the temporal variation of organic seston in 2005, and the same multiple planned comparison tests identified specific differences among dates. A t-test was used to compare the strength of individual byssal threads between dates.

For the 2004 and 2005 data, simple Pearson correlations were used to evaluate the relation between mussel attachment strength and individual factors, which are for 2004: temperature, wind velocity and gonad index, and for 2005: temperature, turbulence, significant wave height (H_s), gonad index, organic seston, current velocity and wind velocity. Additionally, for 2004 and 2005, a forward stepwise multiple regression was used to create a model using the most significant factors, within those cited above, to explain the variations of the response variable (attachment strength). For the multiple regression with 2004 data, gonad index was log-transformed to linearize the relation to attachment strength and no collinearity was found between the three factors ($r < 0.462$). The percentage of the variation in attachment strength explained by each factor was calculated as their specific (standard coefficient * correlation coefficient) * 100 (Vincent 2000). For the 2005 multiple regression analysis, gonad index, organic seston, turbulence and significant wave height were log-transformed to linearize the relation between the explanatory factors and the response variable. Collinearity was found between temperature and turbulence, gonad index, and wind velocity ($r = -0.665, -0.645, -0.704$ respectively) (Table 1). Thus a second multiple regression analysis was conducted without temperature. This multiple regression

analysis was also performed with another probability threshold (0.20 instead of 0.05) to include a second factor in the model (Quinn and Keough 2002).

Table 1. Pearson correlation matrix with correlation coefficient between all the factors, in 2005. (Hs: significant wave height)

	Temperature	Turbulence	Hs	Gonad index	Oganic seston	Current velocity	Wind velocity
Temperature	1.000						
Turbulence	-0.665	1.000					
Hs	-0.405	0.344	1.000				
Gonad index	-0.645	0.313	0.120	1.000			
Oganic seston	-0.107	0.560	-0.194	-0.156	1.000		
Current velocity	-0.024	-0.085	0.048	0.182	-0.068	1.000	
Wind velocity	-0.704	0.472	0.101	0.408	0.010	-0.235	1.000

The mean attachment strength for a given sampling date was related to the mean values of the previous week (seven days before) for the environmental parameters (current velocity, turbulence, temperature, wind velocity, waves height) then reflecting the change of environmental factors between two sampling dates. But for organic seston and gonad index, the value of the same sampling date was used. These data forms were used in all the analysis and figures showing the relationship between the factors and attachment strength.

To explore the possibility that the wind velocity could be used as a surrogate for water turbulence, a simple regression analysis was used to evaluate the relationship between hourly values measured for both factors in 2005.

1.3 RESULTS

1.3.1 *Results for 2004*

In the preliminary 2004 study, attachment strength showed significant variations during the sampling period (Table 2a). A decrease in attachment strength was observed at the beginning of the sampling period (from June 25 to July 19) with a significant difference ($t_{(88)} = 3.04$, $P = 0.003$) between July 5 and 12 (Figure 6a). Attachment strength was generally low during the summer (mean = 22.5 N, between June 25 and August 30), then increased steadily from the beginning of September up to a peak at 42.6 N in mid-October, the last sampling date (Figure 6a). Gonad index also showed significant variations during the sampling period, but no significant differences between two successive dates were revealed with the t-tests (Table 2b; Figure 6b).

Table 2. Hierarchical ANOVAs measuring the differences between dates in 2004, for a) attachment strength (AS) and b) gonad index (GI).

N= 644 (AS and GI were square- transformed)

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>
a) AS				
Date	14	12.069	7.946	< 0.001
Sleeve (date)	30	1.519	2.060	0.001
Error	599	0.737		
b) GI				
Date	14	0.021	2.340	0.025
Sleeve (date)	30	0.009	1.560	0.030
Error	599	0.006		

Temperature varied between 10.3 and 20.6°C during the sampling period, with higher values from mid-July to the end of August and then it decrease in the fall (Figure 6c). Wind velocity was relatively constant until the end of August, when it increased until the beginning of October (Figure 6d).

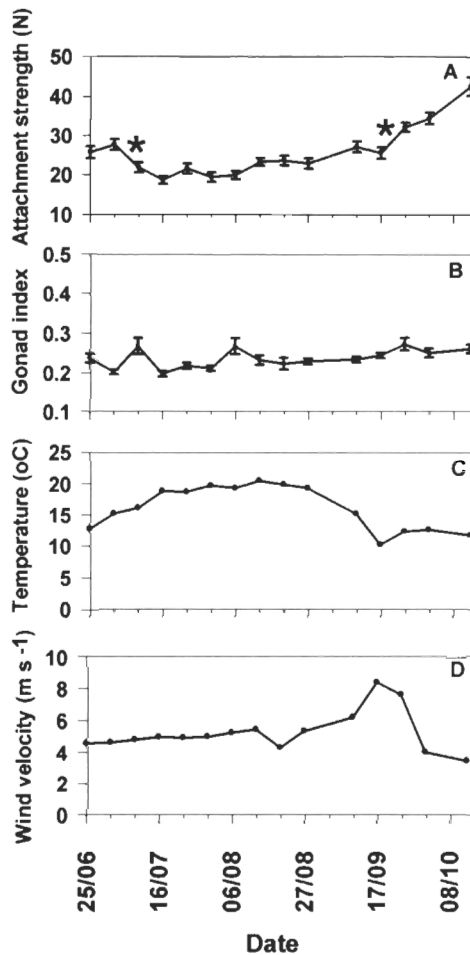


Figure 6. Weekly values of : a) attachment strength (mean \pm s.e) b) gonad index (mantle dry weight (DW): whole tissue DW) (mean \pm s.e); c) temperature and d) wind velocity, during the sampling period from June 25 to October 15, 2004. A star between two successive dates indicates a significant difference revealed by a planned comparisons using a t-test followed by a Bonferroni correction. N= Newton

1.3.2 Relationship with attachment strength (2004)

The correlation between each factor and attachment strength (gonad index, temperature and wind velocity) was revealed by simple Pearson correlations. Temperature was the only factor significantly correlated to attachment strength and both factors were inversely related (Table 3). Gonad index was the second most correlated factor to attachment strength although not significantly. A forward stepwise multiple regression analysis was conducted to examine the relative importance of each factors. Temperature was the first factor to be entered in the model and it explained 52% of the attachment strength variation. The regression stopped at the second step after the addition of wind velocity and the model including these two factors explained 61% of the attachment strength variability (Table 4). Moreover, the proportion of the variation explained by temperature (60.2%) was more important than by the wind velocity (6.2%) (Table 3 and Table 4).

Table 3. Simple Pearson correlations between each explanatory factor and attachment strength in 2004. N=15

Factors	<i>r</i>	<i>P</i>
Temperature (°C)	-0.72	0.015
Gonad index	0.45	0.545
Wind velocity (m s ⁻¹)	-0.16	1.000

Table 4. Results of a forward stepwise multiple regression with attachment strength as the response variable and temperature, wind velocity and gonad index, as explanatory variables in 2004. Adjusted $R^2 = 0.607$, $N = 15$

Regression step no.	Source of variance	Standard coefficient	<i>P</i>
1	Temperature	-0.835	0.001
2	Wind velocity	-0.396	0.043

1.3.3 Results for 2005

The 2004 results were used to steer the 2005 study, which was more extensive and complete in terms of sampling duration and characterization of the environmental parameters, namely the hydrodynamic conditions.

1.3.4 Attachment strength (2005)

The attachment strength of *M. edulis* varied considerably and significantly during the sampling period in 2005 (Figure 7a; Table 5a). It was high in late May-early June and decreased quickly and significantly (32% decrease from 40.0 to 27.3 N) in late June ($p < 0.001$ between June 20 and 27; Figure 7a). In the summer, the attachment strength remained relatively weak with no significant differences between two successive dates until

the beginning of September, then attachment strength increased steadily (from 24.1 to 46.6 N) until the end of the sampling period.

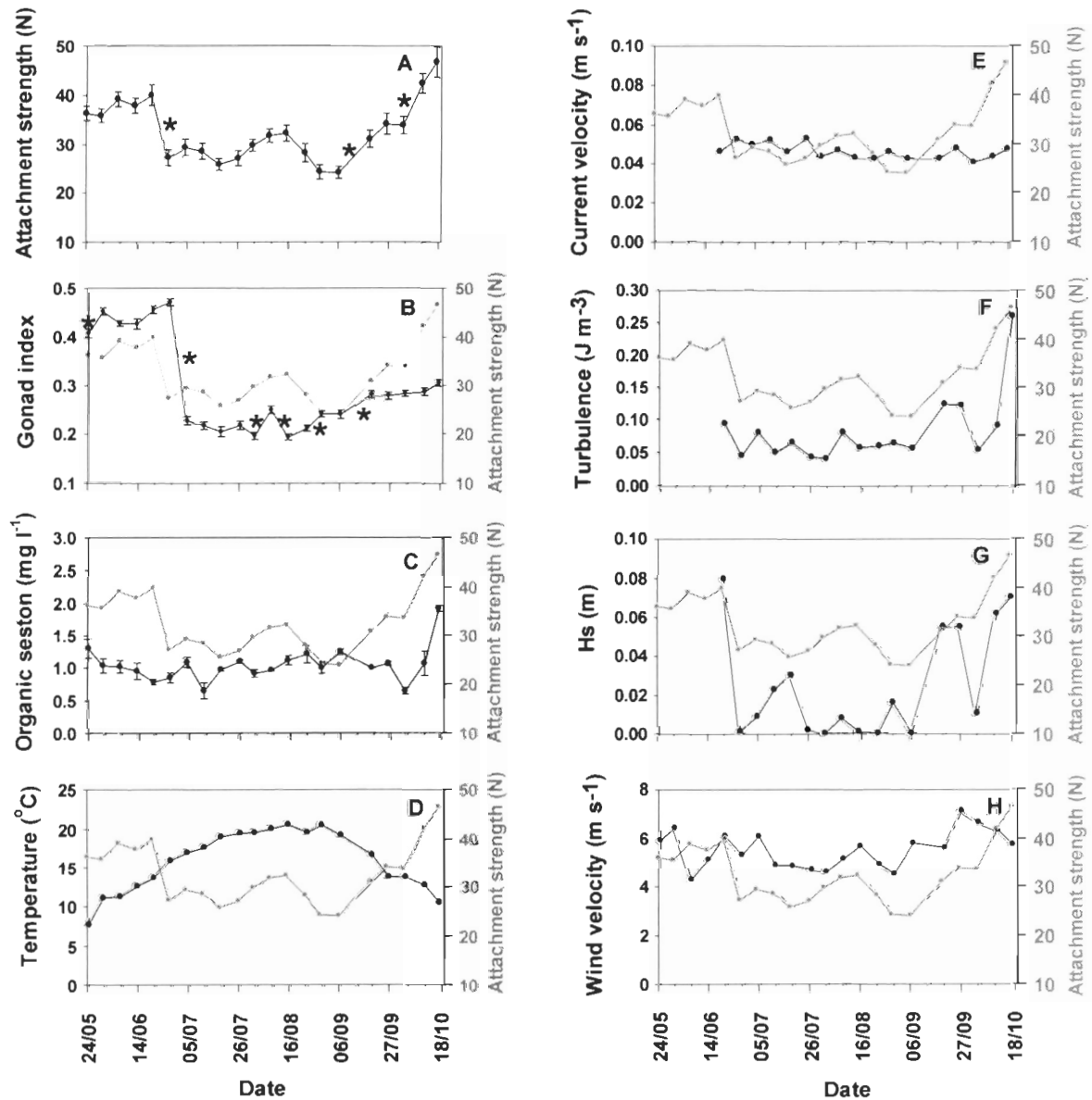


Figure 7. Weekly values measured in 2005 : a) attachment strength (mean \pm s.e.); b) gonad index (mean \pm s.e.) c) organic seston (mean \pm s.e); d) water temperature; e) current velocity; f) turbulence; g) significant wave heights (Hs); h) wind velocity. A

star between two successive dates indicates a significant difference revealed by a planned comparisons done with a t-test followed by a Bonferroni correction.

Attachment strength data has been superposed as a shaded curve in graphs b- h to facilitate the results examination

Table 5. Hierarchical ANOVAs measuring the differences between dates in 2005, for a) attachment strength (AS) and b) gonad index (GI).

N= 630 (AS and GI were log- transformed)

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>
a) AS				
Date	20	1.076	5.974	<0.001
Sleeve (date)	42	0.180	2.286	<0.001
Error	567	0.079		
b) GI				
Date	20	6.390	113.467	<0.001
Sleeve (date)	42	0.056	1.150	0.244
Error	567	0.049		

1.3.5 *Individual force of byssal threads (2005)*

The strength of individual byssal threads was measured in summer (August 2) and in fall (October 17) when mussel attachment strength was weak and strong, respectively. The force needed to break the individual threads was significantly different ($t_{(16)} = 3.61$, $P = 0.001$) between the two periods and threads were almost 52% stronger in the fall (0.50 N) than in the summer (0.33 N) (Figure 8).

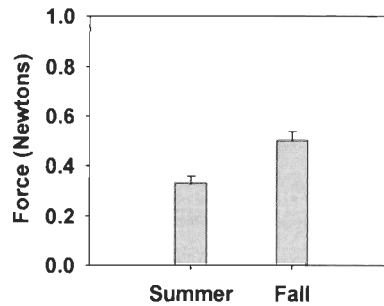


Figure 8. Force (mean \pm s.e.) needed to break individual byssal threads on August 2 (summer) and October 17 (fall), 2005 (N=35)

1.3.6 *Reproductive condition (2005)*

Reproductive condition, characterized by the gonad index, also varied significantly during the sampling period (Table 5b). Gonad index decreased significantly from 0.47 to 0.22 at the end of June, a 53 % reduction ($P < 0.001$ between June 27 and July 4; Figure 7b). Gonad index remained low all summer long and increased slowly in fall until the end of the sampling period.

1.3.7 *Environmental data (2005)*

The organic seston showed an overall significant variation during the sampling period but with no particular pattern other than an increase at the beginning of October. (Table 6; Figure 7c). Mean weekly temperature in the lagoon ranged from 8 to 21°C with the highest

values in July-August when attachment strength was low (Figure 7d). Current velocity was weak during the sampling period and showed no important variations (values between 4 and 6 cm s^{-1}) (Figure 7e). Both turbulence and significant wave height were low in the summer and increased sporadically from the beginning of September (Figure 7f and g). The significant wave height values were sometimes zero because this parameter was recorded near the bottom of the lagoon, so that small waves did not reach the bottom and were not recorded (Figure 7g). The wind velocity, whatever its direction, did not show any particular pattern except an increase at the end of the sampling period (Figure 7h).

Table 6. One-way ANOVA for organic seston

differences between dates in 2005, N= 63

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>
Date	20	0.220	7.985	< 0.001
Error	42	0.028		

1.3.8 Relationship with attachment strength (2005)

The relationship between each factor and attachment strength of mussels was measured by simple Pearson correlations (Table 7). All factors except the organic seston concentration, wind velocity and current velocity were significantly correlated to the attachment strength. Temperature was the factor with the highest relationship to attachment

strength, and both factors were inversely related. Turbulence was highly and positively correlated to attachment strength followed by significant wave height and gonad index.

Table 7. Simple Pearson correlations relating the attachment strength of mussels with each explanatory factor in 2005. N= number of weekly measurements, r = correlation coefficient. Turbulence, Hs, gonad index and organic seston were log-transformed

Factors	N	r	P
Temperature (°C)	21	-0.79	<0.001
Turbulence ($J\ m^{-3}$)	17	0.72	0.001
Significant wave height (H_s)	17	0.56	0.024
Gonad index	21	0.54	0.012
Organic seston ($mg\ l^{-1}$)	21	0.28	0.225
Current velocity ($m\ s^{-1}$)	17	-0.14	0.598
Wind velocity ($m\ s^{-1}$)	21	0.38	0.087

A first stepwise multiple regression analysis was done with all factors (temperature, turbulence, gonad index, significant wave height, wind velocity, current velocity and organic seston). This analysis excluded the first 4 experimental weeks due to missing data about turbulence, wave height and current velocity (Table 8). This procedure stopped at the first step with temperature retained as the only significant factor explaining 65.5% of the variability of the attachment strength (Table 8). This result was explained by the observed inverse pattern between the temperature and the attachment strength (Figure 7d).

Because collinearity was found between temperature and turbulence, gonad index, and wind velocity (Table 1), the analysis was performed again but without temperature. In this second multiple regression analysis, turbulence was the only variable introduced in the model and it explained 49.1% of the variation in attachment strength (Table 8). When the stepwise analysis was forced to enter two factors in the model, gonad index was the only other factor to be included in the model, but it was not significant ($P = 0.20$).

Table 8. Forward stepwise multiple regression analyses done with attachment strength as response variable and all the factors as explanatory variables (regression no. 1) and all the factors except temperature as explanatory variables (regression no. 2), in 2005. N=17

Regression no.	Factors	Regression step no.	Source of variance	Adjusted R^2	Partial r^2	p value
1	All factors	1	Temperature	0.655	0.676	< 0.001
2	Without T°	1	Turbulence	0.491	0.523	0.001

1.3.9 Wind-turbulence relationship (2005)

Water turbulence seemed to have an important influence on the variation of attachment strength but these data are not easily accessible. So the relationship between

turbulence and wind velocity was evaluated to explore the possibility to use the latter as a proxy in further studies and to look at the 2004 data when no turbulence data were recorded. Indeed, almost 50% of the turbulence measured at 6 m from the surface was created by wind velocity (whatever its direction) and both factors were related according to an asymptotic relationship (Figure 9). Wind velocity increased in the fall, while water turbulence reached peak values twice during the sampling period: September 12 and October 16 (Figure 10a). During these peaks of turbulence, the wind velocity was also higher than usual (Figure 10b,c) and its direction was approximately North and East, respectively.

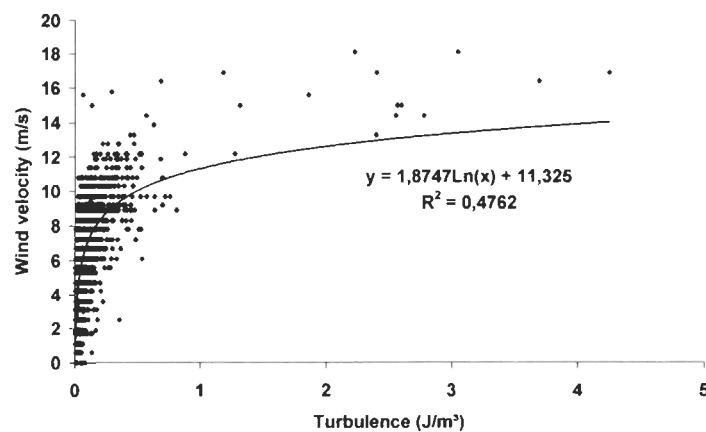
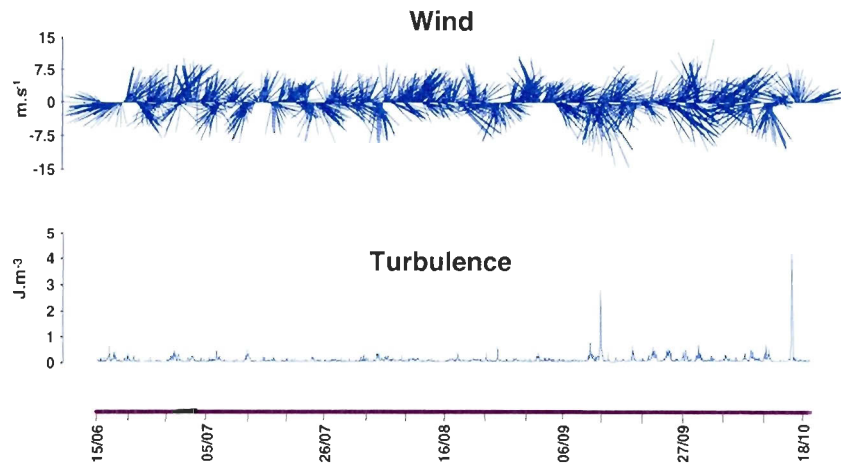
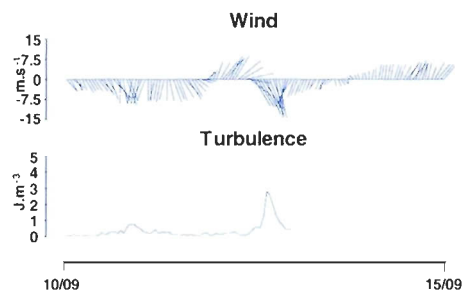


Figure 9. Relationship between the turbulence recorded by the ADV near the lagoon bottom and the wind velocity in 2005

a)



b)



c)

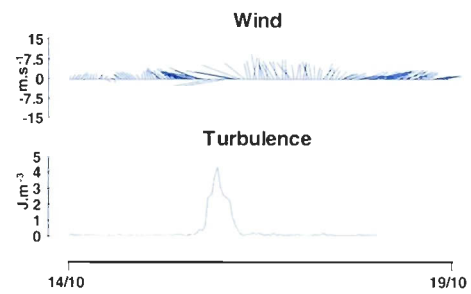


Figure 10. a) Wind and turbulence throughout the sampling period are represented by daily means. b) Wind and turbulence around September 12 as hourly means and c) Wind and turbulence around October 16 as hourly means. Wind velocity is indicated by the length of the arrows and direction by its angle relative to the North (North is perpendicular to the x axis and pointed up)

1.4 DISCUSSION

There was an important variation of the attachment strength in suspension-cultured mussels (*M. edulis*) from June to October 2005 in a sheltered lagoon of the Magdalen Islands with almost a two-fold increase in fall (September-October) relatively to summer. Such a two-fold increase was also measured in the preliminary experiment in 2004. Similar variation in attachment strength of wild mussels, following a seasonal cycle, has also been observed on Rhode Island shores (Carrington 2002b, Moeser and Carrington 2006), in Nova Scotia (Hunt and Scheibling 2001), in the UK (Price 1982), and in South Africa (Zardi *et al.* 2007). Carrington (2002b) found a similar pattern to the present study with values of tenacity (attachment strength/planform area) increasing twofold in fall/winter relatively to summer. Although the present study covered a shorter period (< six months each year), it is unique for its higher sampling frequency compared to the previous studies i.e. weekly rather than monthly samplings. This higher sampling frequency provided a more precise picture of attachment strength transitions between the seasons. In 2005, there was a very steep decline in attachment strength at the end of June (-32 % in one week) and a gradual increase from the beginning of September until mid-October. A similar pattern was observed in 2004, although the decrease in late June is less evident because no data were collected before June 25. These results confirmed field observations in the Magdalen Islands where mussels are known to be tightly attached to the culture substrate during the spring months but very loosely attached during the summer months before gaining a

stronger attachment in fall (B. Myrand, pers. obs.). The weak attachment during the summer months may thus lead to heavy fall-offs (Bourque and Myrand 2006). Therefore heavy losses in commercial production during summer are probably related to a weaker attachment strength and not solely to mortality or predation (Mallet and Myrand 1995, Myrand *et al.* 2000, Inglis and Gust 2003).

Mussel attachment strength is not only related to the number of byssal threads, but also to the strength of each individual thread (Smeathers and Vincent 1979, Bell and Gosline 1996, Bell and Gosline 1997). Indeed, as attachment strength of the mussel byssus varied seasonally, so did the material properties of the byssus as the threads produced in fall were 52% stronger than in summer (0.50 vs 0.33 N, respectively). Moeser and Carrington (2006) reported a decrease from summer (0.12 N) to fall (0.08 N) for *M. edulis* from Narragansett Bay (RI, USA). Despite this change, they did not observe a significant difference in byssal thread strength between these two periods as in the present study. The difference with our results of the variation of thread strength between summer and fall, could be related to the difference in the sampling dates corresponding to summer and fall. Further, strength values measured here were about 4 times higher than those reported by these authors and it could be related to the difference in mussels size (68 mm, for our mussels compare to 40 mm, for their mussels). As in the present study, the change in individual thread strength followed the same pattern than attachment strength variation. It is unknown what specific factors contribute to these changes in material properties.

1.4.1 *Factors influencing the attachment strength*

In addition to water temperature, the most influential factors on attachment strength in field conditions were water turbulence (hydrodynamic conditions) and mussels reproductive condition.

Temperature seems, at first, to be the most influential factor on attachment strength because of its strong negative correlation ($r = -0.79$) in 2005. This parameter is the only factor retained in the forward stepwise multiple regression model and it explained 65.5% of the variability of the attachment strength. A similar relationship was observed in 2004 ($r = -0.72$) and it was the first factor entered in the multiple regression model and it explained 60.2% of the variability of attachment strength. The temperature varied between 8 to 21°C, in 2005, during the sampling period with higher values in the summer when attachment strength was weak and lower values in the late spring and fall when attachment strength was high. The same pattern has been observed in 2004. This inverse relationship between temperature and attachment strength is in accordance with Carrington (2002b) for *M. edulis* in Rhode Island. However, these results need to be interpreted with caution. First, Price (1982) observed the opposite pattern with a positive correlation between attachment strength of *M. edulis* and temperature on England shores where temperature varied between 10 and 15 °C, with a maximal value of 17 °C in September. Furthermore, a number of laboratory studies showed that the production of byssal threads increase with temperature within a range of 5-25°C (Van Winkle 1970, Young 1985, Selin and Vekhova 2004, Kobak

2006). This positive relationship between temperature and attachment strength (more byssal threads = higher attachment strength) was not evident in this field study, perhaps because threads decay is higher in the summer when temperature is warm (Carrington 2002b). Doing so, temperature could possibly have a direct negative effect on attachment strength through a higher rate of threads decay than threads production.. Further studies on threads decay would be needed for a better understanding of this negative temperature-attachment strength relationship in field conditions.

When a forward stepwise multiple regression was performed without temperature as an explanatory variable, water turbulence became the most important factor acting on attachment strength explaining 50% of its variability. This is due to the high correlation between turbulence and attachment strength ($r = 0.72$). Despite the missing values for the first 4 weeks at the beginning of the sampling period, turbulence followed a similar temporal pattern than attachment strength with low values in the summer and an increase in the fall. Turbulence is a hydrodynamic parameter characterizing the water column and is defined as fluid particles moving in a highly irregular manner with intense small-scale three-dimensional motion (Vogel 1989, Mann and Lazier 2006). Water motion has also been suggested to have an important influence on attachment strength of wild mussels on wave-swept shores (Price 1982, Witman and Suchanek 1984, Bell and Gosline 1997, Hunt and Scheibling 2001, Carrington 2002a, Carrington 2002b, Hunt and Sheibling 2002). This positive relationship was also observed in laboratory as an increase in water agitation or flow velocity triggered threads production and an increase of mussels attachment strength

(Mahéo 1970, Van Winkle 1970, Witman and Suchanek 1984, Young 1985, Lee *et al.* 1990, Dolmer and Svane 1994, Alfaro 2005). As suspension-cultured mussels in the present study were kept in the water column, at 2 m below the surface, it is likely that hydrodynamic parameters acting in the lagoon do not influence the attachment strength of mussels in the same way as in the intertidal zone. However, turbulence seemed to be the most influential hydrodynamic parameter on the attachment strength of mussels in the well-mixed water column of this shallow lagoon (Koutitonsky *et al.* 2002). Water turbulence seemed to influence the attachment strength of cultured mussels throughout most of the sampling period.

Reproductive condition is another factor that seemed to have an important influence on the attachment strength of the cultured mussels. This factor, characterized by the gonad index, was significantly correlated to attachment strength in 2005 ($r = 0.56$). Indeed a massive spawning, as shown by a 53% decrease in the gonad index over a single week (from 0.47 to 0.22), occurred almost simultaneously (during the following week) with a drastic decline in attachment strength (-32%) in late June-early July 2005. This is the usual period of mass spawning for suspension-cultured mussels in Eastern Canada (Mallet and Myrand 1995) and such an important decrease in gonad index is in agreement with reported losses of up to 50% in total soft tissues during the spawning of large mussels (Bayne and Worrall 1980, Kautsky 1982, Mallet and Myrand 1995). This dramatic decline of gonad index at the end of June was not apparent in 2004, most likely because sampling started one month later than in 2005, probably after the mass spawning. Indeed, the correlation

between gonad index and attachment strength ($r = 0.45$) in 2004 was not significant. Reproductive condition was not retained in the multiple regression model possibly because there was a one week lag between the decreases of attachment strength and the gonad index in 2005. Further, the multiple regression analysis could not include the results from the first 4 weeks of the sampling period, when both the gonad index and the attachment strength showed high values, because data about hydrodynamic parameters were lacking. However, when the probability threshold was forced to $P = 0.20$ in the multiple regression, the only factor added to the turbulence in the model was the gonad index.

Although reproduction requires an important energy input for gamete production (Bayne *et al.* 1982, Bayne *et al.* 1983, Thompson 1984, Lemaire *et al.* 2006) it did not influence negatively the attachment strength of the cultured mussels as shown in other studies (Carrington 2002b, Zardi *et al.* 2007). Indeed mussels can allocate as much as 90% of their energy to gamete production (Rodhouse 1984, Seed and Suchanek 1992) while byssal threads production can represent 8% of a mussel's monthly energy expenditure (Hawkins and Bayne 1985). So when available energy is limited, the mussel must choose between competing physiological functions for its allocation : metabolism, growth, gamete production, byssal thread production (Bayne and Newell 1983). Some studies on wild mussels observed a trade-off between gamete production and attachment strength (Carrington 2002b, Zardi *et al.* 2007). These authors stated that byssal threads production may only be possible when energy is available, i.e. when there is no gamete production. However, there is no such trade-off in this study as attachment strength was high during a

period of 4 weeks preceding the mass spawning, i.e. during the last phase of the gametogenesis. Further, attachment strength was weak in the summer during the resting period which follows spawning. The difference observed between the present and the previous studies may be related, at least partly, to the weekly sampling which provided a more precise picture in this study. We can also hypothesize that the available energy (food quantity and quality) was not limited at the experimental site (Mallet and Myrand 1995) during gametogenesis, so that byssal thread production could occur concurrently with gametogenesis with no needs for trade-offs. Moreover, gametogenesis occurred in early summer when temperature was not at its peak so that threads decay could be at a low level (Carrington 2002b) thus leading to lower needs for the production of new byssal threads.

The major decrease in attachment strength occurred rapidly and almost simultaneously with the massive spawning. The decrease in attachment strength occurred anytime between June 20 and June 27 while spawning occurred somewhere between June 27 and July 4. Thus both events could have occurred almost simultaneously and a daily sampling would have been useful to better define the relationship between both factors. To our knowledge, no other studies reported such a synchrony between a sharp decrease in attachment strength and spawning. Indeed, in the open water near the Magdalen Islands, a drastic decline of attachment strength and gonad index of suspension-cultured mussels occurred simultaneously (Lachance *et al.*, unpubl. data). As threads decay usually takes about 4-6 weeks (Carrington 2002b), this sharp decline in attachment strength within one week suggests that numerous threads were “lost” in a short period of time near or during

spawning. Mussels possibly sever their own byssal threads (Mahéo 1970, Price 1983, Lee *et al.* 1990, Hunt et Sheibling 2002) or threads decay was accelerated at this moment. After having invested large amounts of energy in the gamete production, spawning is known to be a stressful event which can weaken the mussels and even lead to massive mortality (Worrall and Widdows 1984, Mallet and Carver 1993, Mallet and Myrand 1995, Myrand *et al.* 2000). For example, digestive cells of the digestive tubules of mussels show disruption of their structure and evidence of autolysis after spawning (Bayne *et al.* 1978). This could decrease their ability for food absorption and thus limit their energy intake. As a result, less energy could be available for the production of new byssal threads for a certain period of time after spawning thus contributing to a low attachment strength at this moment..

Food concentration had no significant influence on attachment strength. Organic seston concentration showed no particular cycle and values were relatively stable (~1 mg/l) during the sampling period, except for an increase (up to 2 mg/l) in fall corresponding probably to a phytoplankton bloom. These values are in agreement with typical values found in the Magdalen Islands lagoons (Myrand 1991, Mallet and Myrand 1995). Food availability is known to influence byssal threads production as starved mussels decrease their thread production (Price 1980, Young 1985, Clarke 1999). In contrast to these studies, the increase in organic seston concentration in October occurred after the attachment strength began to increase (September) in the lagoon. Thus food availability was not a major factor driving the variation of attachment strength of cultured mussels at the experimental site. This may be the result of a low variability in the seston concentration

during the sampling period. Moreover, as discussed before, the material properties of the byssal threads changed seasonally in the present study and that could have influenced the attachment strength of the mussels. However, this change in properties leading to stronger threads neither was probably related to food concentration. In fact, Monahan and Wilker (2004) suggested that factors influencing the material properties of byssal threads are present in the water chemistry rather than in food.

The low current velocities measured in the lagoon had no impact on attachment strength. Throughout the sampling period, current velocity varied only between 4 and 6 cm s⁻¹ where mussel sleeves were held in suspension. That was in agreement with previous measurements of current velocity (< 5 cm s⁻¹) in this lagoon (Koutitonsky *et al.* 2002). Dolmer and Svane (1994) showed no difference in threads production between still water and currents at 7.7 cm s⁻¹, but production increased at 19.4 cm s⁻¹. Current velocity was not correlated to attachment strength probably because it was weak and showed very little variation. In contrast, studies on wild mussels from the intertidal zone showed that the number of byssal threads increased with current velocity (Lee *et al.* 1990, Dolmer and Svane 1994, Hunt and Sheibling 2002, Alfaro 2005).

Wave action, which is characterized by significant wave height, was significantly correlated to attachment strength. As discussed above, wave action is a dominant factor in the intertidal environment and it enhances thread production (Price 1982, Witman and

Suchanek 1984, Bell and Gosline 1997, Carrington 2002b). However, attachment strength was more strongly correlated to turbulence than significant wave height even though both are mostly the results of the wind action (Open University 1989, Kjerfve 1994, Mann and Lazier 2006). Wave action is probably not influencing wild mussels in the intertidal zone in the same way as the suspension-cultured mussels. Cultured mussels are kept suspended in the water column and are thus primarily influenced by turbulence rather than by the height of the waves. Wave action was also possibly underestimated in the present study because waves were recorded near the bottom of the lagoon (6 m from the surface) and thus were smaller than at the sleeves depth (2 m from the surface).

1.4.2 *Wind-turbulence relationship*

Wind velocity is the major source of water turbulence (Mann and Lazier 2006) and may serve as a proxy when no turbulence data are available like in the 2004 preliminary experiment. Turbulence is an important factor driving the variation of attachment strength of mussels but its measurement is not always possible because it needs specialized equipment and specific expertise. In 2005, the relationship between wind velocity and turbulence at the experimental site was examined. Both increased in the fall and there were important increases in wind velocity when turbulence peaked. The mixing of the water column is provided essentially by wind action in this kind of shallow lagoon (Kjerfve 1994, Koutitonsky *et al.* 2002). Whatever its direction, wind velocity explained 50% of the turbulence measured at the experimental site near the bottom of the lagoon in 2005. As the

mussel sleeves were suspended at 2 m from the surface, we can hypothesize that the impact of the wind velocity on turbulence could be higher than measured near bottom since the effects of the wind on the particles in the water decrease with depth (Kjerfve 1994). In contrast to turbulence, wind velocity was not significantly correlated to the attachment strength of mussels in 2005. However, even if the wind velocity was not significantly correlated to attachment strength in 2004, this factor was retained in the multiple regression model explaining 6.2% of the attachment strength variability and showed a similar increase in fall than attachment strength. This weak relationship between wind velocity and attachment strength could be probably due to the indirect impact of the wind on mussels kept suspended in the water column. Indeed, the direction of the wind could influence the impact on the mussel sleeves. For example, southerly winds are partly blocked by the House Harbour Island. Nevertheless, wind velocity showed a general pattern similar to attachment strength in 2004 and 2005.

1.5 CONCLUSION

In conclusion, this is the first study to examine the attachment strength of suspension-cultured mussels and also the first to study temporal changes of the attachment strength in field conditions based on weekly samplings. The attachment strength of mussels varied twofold from summer to fall. The individual force of byssal threads also increased substantially in fall compared to summer, contributing to the increase of attachment strength. The water temperature was the factor with the highest correlation with attachment

strength and this was an inverse relationship. A higher temperature could increase the byssal threads decay during the summer and then lead to a lower attachment strength. After water temperature, turbulence was the second factor with the highest correlation with attachment strength. This latter factor seemed to influence attachment strength after the massive spawning in early summer. Mussels did not attach firmly to the sleeves in the summer when turbulence is low, but they increased their attachment strength with the increase of turbulence in fall to provide against their dislodgement. Reproduction seemed to have an impact on attachment strength as a mass spawning occurred almost synchronously with a major decrease in attachment strength in late June. This was the first time spawning seemed to be so closely synchronized with a major decrease in attachment strength. Wind velocity is related to turbulence and thus can provide information relatively to the influence of turbulence on the attachment strength of mussels. Mussels growers should be careful when they harvest during the spawning period and the summer period to minimize possible fall-offs due to the weakening in mussel attachment.

1.6. ACKNOWLEDGEMENTS

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CONCLUSION GÉNÉRALE

La présente étude avait pour but premier d'évaluer la variation temporelle de la force d'attachement des moules de culture (*Mytilus edulis*) aux Îles de la Madeleine situées dans le Golfe du St-Laurent, Canada, et de déterminer les facteurs pouvant l'influencer. Les résultats corroborent les observations concernant des chutes de moules plus importantes durant l'été dans les lagunes des Îles de la Madeleine. En effet, la force d'attachement des moules est deux fois plus faible en été qu'en automne dans la lagune du Havre-aux-Maisons. Les facteurs qui semblent influencer le plus la force d'attachement des moules, après la température, sont la turbulence de l'eau et l'état reproducteur des moules. La température de l'eau était négativement corrélée avec la force d'attachement, ce qui pourrait être expliqué par une accélération de la dégradation des filaments de byssus lorsque la température augmente. La ponte des moules semble coïncider avec la diminution drastique de la force d'attachement à la fin du mois de juin, pouvant être dû à l'effet global du stress de la ponte sur le métabolisme de la moule. La turbulence semble influencer la force d'attachement une fois que la moule a pondu puisque les deux paramètres (turbulence et force d'attachement) suivent le même patron durant l'été et l'automne. Ceci s'explique par le fait que la moule doit s'attacher plus fermement en automne, lorsque la turbulence de l'eau augmente, pour résister au mouvement de l'eau qui risque de la détacher. Ces résultats apportent des connaissances inédites sur la force d'attachement des moules de culture en suspension dans l'eau puisque cette étude est la première à s'intéresser à ce sujet et à l'avoir étudié sur une base hebdomadaire.

Les résultats de la présente étude apportent également de nouvelles connaissances pouvant servir directement aux mytiliculteurs. En effet, bien que l'on ne puisse pas avoir un impact direct sur les facteurs influençant la force d'attachement des moules, des stratégies peuvent être mises en place afin de réduire leurs effets en effectuant un suivi de la condition de reproduction des moules ainsi que de la vitesse des vents qui est corrélée avec la turbulence de l'eau. Ainsi, la manutention des lignes (entretien général, ajout de bouées...) et la récolte seraient à effectuer avec précaution, à partir ou très près du moment de la ponte des moules. Il faudrait également être conscient que les moules sont moins bien attachées durant une période de vents plus calmes, et donc de plus faible turbulence dans la colonne d'eau.

Cette étude contribue également à l'ajout de nouvelles connaissances au niveau des impacts environnementaux sur l'habitat benthique des sites d'élevage en suspension de moules. En effet, la chute de moules sur le fond située sous les filières d'élevage peut avoir des impacts sur la structure de la communauté benthique en augmentant l'enrichissement organique du sédiment ainsi que l'attraction des prédateurs à ces sites (Grant *et al.* 1995, Inglis and Gust 2003, Leonard 2004). De ce fait, les nouvelles connaissances apportées par la présente étude sur la variabilité temporelle de la force d'attachement des moules de culture ainsi que sur les facteurs qui l'influencent s'ajoutent aux connaissances sur la variabilité de la structure benthique aux sites d'élevage de moules en suspension.

Il pourrait être pertinent d'effectuer des études plus poussées sur les changements temporels du taux de décomposition des filaments et de l'influence de la température sur celui-ci. En effet, ce facteur souvent négligé (les études portant surtout sur le taux de sécrétion des filaments) pourrait avoir une influence non négligeable sur la force d'attachement des moules. De plus, une étude portant sur la mesure de la force d'attachement en période hivernale, lorsque la température est basse et qu'il y a un couvert de glace stable sur les lagunes, pourrait apporter des informations supplémentaires sur l'effet relatif de la température et de la turbulence sur la force d'attachement des moules.

L'élevage en mer commence à prendre son essor au Québec. Il serait intéressant d'effectuer une étude comparable sur la force d'attachement des moules élevées en pleine mer puisque les paramètres environnementaux y sont différents, ce qui pourrait entraîner des différences au niveau de la force d'attachement des moules et donc des pertes éventuelles. On sait, par exemple, que le cycle reproducteur et l'intensité de la ponte diffèrent chez les moules en élevage en lagune et en mer aux Îles de la Madeleine (Gauthier-Clerc *et al.*, comm. pers.). Il est aussi bien évident que les conditions de turbulence et de température sont très différentes dans ces deux environnements.

La méthode utilisée, dans la présente étude, pour mesurer la force d'attachement des moules en culture en suspension sur des boudins à l'aide d'un dynamomètre a permis de

mesurer cette force directement, sans détacher les moules de leur substrat qu'est le boudin. Cette méthode nous a donc permis d'avoir une véritable mesure de la force d'attachement et non une mesure de la capacité de rattachement (où les moules auraient été préalablement détachées du boudin). Par contre, cette méthode devait se limiter à la mesure de la force d'attachement des moules en périphérie du boudin. Il n'était pas possible de penser mesurer la force d'attachement des moules localisées plus à l'intérieur du boudin, par exemple celles présentes le long de la corde de support, sans perturber l'assemblage des moules et donc de modifier les conditions globales d'attachement. Les conclusions tirées de l'étude se limitent donc aux moules en périphérie des boudins puisque les individus se retrouvant à l'intérieur du boudin peuvent être influencés par d'autres facteurs telle qu'une diminution de la disponibilité en nourriture que nous n'avons pu évaluer ou encore une accumulation de limon, détritiques et fèces provenant de l'ensemble des organismes sur le boudin et qui pourraient causer une entrave à un attachement solide au substrat. De plus, la force d'attachement mesurée pour un individu ne correspondait pas à sa seule force individuelle puisqu'il était entouré de congénères qui pouvaient aussi fixer des filaments de byssus sur sa coquille pour ainsi créer un réseau favorisant un meilleur ancrage. Par conséquent, l'approche utilisée a mesuré la force d'attachement globale d'un individu, i.e. sa propre force couplée à celle des congénères qui l'entourent et qui contribuent aussi à son attachement. Cette méthode de mesure représente bien la réalité puisque, que ce soit en zone intertidale ou sur boudin d'élevage, les moules s'attachent aussi les unes aux autres et leur force d'attachement dépend donc également de l'action de leurs voisines. La méthode pourrait être améliorée en développant une façon de mesurer la force d'attachement des

moules situées à l'intérieur du boudin. De plus, si une mesure de force d'attachement individuelle est réellement souhaitée il pourrait être préférable d'élaborer une façon d'éliminer l'influence de la fixation des congénères. Par contre, cette méthode fournirait des résultats plus théoriques puisque les conditions de mesure seraient artificielles, mais elle pourrait toutefois être utile pour une meilleure compréhension des mécanismes en jeu. Malgré ces éléments limitants, la méthodologie utilisée dans la présente étude a permis de déterminer de façon précise et rigoureuse la variabilité temporelle de la force d'attachement des moules en culture en suspension ainsi que les facteurs qui l'influencent.

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